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TEMPORAL VARIATION IN THE SELECTED HABITATS OF A GUILD OF GRASSLAND SPARROWS

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The selected habitats of grassland birds have been the source of much study (Cody 1968; Wiens 1969, 1973, 1974; Whitmore and Hall 1978). Since the structural character of the habitat is important in the selection mechanism (Hildén 1965, Verner 1975), quantification of bird species distribution on numerous habitat variables has often given insight into species specific requirements.

Wiens (1973) suggested that the time of occupancy of territories may have an effect on site selections. Early arriving Grasshopper Sparrows (*Ammodramus savannarum*) occupied habitats structurally different from those of Savannah Sparrows (*Passerculus sandwichensis*). However, the distinctions between initial habitats were lost as bird densities increased. Lacking fitness data he was unable to determine what effect this had on the ecology of the 2 species. His results imply that habitat, at least in his study area, may be limiting and that the species are forced together as their densities increase. One question that might be asked is that if habitat is not abundant and the species do have to coexist in identical, or nearly so, habitats, what effect does change in the structure of the vegetation during territory occupancy have on the community relationships of the species?

In this study I examine the effect of vegetation growth from spring through summer on the selected habitats of 3 grassland sparrows: the Grasshopper, Savannah and Vesper (*Pooecetes gramineus*) sparrows. To my knowledge such temporal variation in selected habitats has not been investigated for birds, as, in the past, most attempts to relate vegetation structural variables to species have been done only during the "peak of the breeding season."

STUDY AREAS AND METHODS

Current surface mine reclamation procedures have, in many eastern states, created tracts of grassland which are not unlike the Great Plains, at least in avifaunal composition. Such tracts are a new resource for birds and in areas such as northern West Virginia species not abundant in the east are common (Whitmore and Hall 1978).

This study was conducted on several recently reclaimed surface mines in Preston County, West Virginia, at an elevation of ca. 640 m. After coal removal the area was regraded, treated with fertilizer and soil stabilizers and planted with a mixture of tall fescue (*Festuca arundinaceae*), red top (*Agrostis alba*), oats (*Avena sativa*), Timothy (*Phelum pratense*), and birds-

TABLE 1

LIST OF VEGETATION STRUCTURE VARIABLES MEASURED WEEKLY ON THE TERRITORIES OF GRASSLAND SPARROWS; STATISTICAL SIGNIFICANCE AS DETERMINED BY ANOVA OF SPECIES AND TIME DIFFERENCES AND DIRECTION OF CHANGE ARE ALSO INDICATED

Variable	Species	Time	Species × time	Direction of change
Percent basal area cover of grass	*[1]	**[2]	NS[3]	–
Percent forb cover	NS	**	NS	+
Percent litter cover	*	**	NS	+
Percent bare-ground cover	NS	**	NS	+
Litter depth (in cm)	*	NS	NS	NC[4]
Forb height (in cm)	NS	**	NS	+
Effective height (in cm)	NS	**	NS	+
Vertical density of grass	*	**	NS	+
Vertical diversity of grass	NS	**	NS	+
Horizontal diversity of grass	NS	**	NS	+
Total grass density	NS	**	NS	+

[1] * = $P < 0.05$.
[2] ** = $P < 0.01$.
[3] NS = not significant.
[4] NC = no change.

foot trefoil (*Lotus corniculatus*). As natural succession begins, other grass species, including orchard grass (*Diactylis glomerata*), poverty grass (*Danthonia spicata*), velvet grass (*Holcus lanatus*) and rye grass (*Lolium perenne*), become established (Staples 1977).

During the first week of May 1977, territories of Grasshopper, Savannah and Vesper sparrows were located by the territory flush technique (Wiens 1969). The center of the territory was marked and served as the starting point for 2 line transects 25 m in length, the directions of which were determined by a random numbers table and a compass. Several vegetation structure variables were measured on each territory weekly for 11 weeks (Table 1). For the most part the territories were occupied throughout the study period and when the study was terminated on 25 July, most of the sites still had birds on them, although intraspecific defense was not nearly as intense as in earlier weeks.

Multivariate analysis of variance (MANOVA) and discriminant function analysis (DFA), as well as univariate analysis of variance (ANOVA) were used to analyze these data. Following the procedures of Harner and Whitmore (1977) p-dimensional niche overlap (habitat use) values were calculated for each species pair, as defined on the habitat structural variables, using the density overlap method, an adaptation of DFA. This measure varies between 0 and 100% with 0% being no overlap and 100% being complete overlap.

RESULTS

Territories of the sparrows showed significant differences in 4 vegetation variables throughout the 11 week study period (Table 1): (1) basal area cover of grass, (2) litter cover, (3) litter depth, and (4) vertical grass density. This means that their territories were different from each other in these structural aspects at the time of initial occupancy as well as in late July. The other variables were not different over the entire period.

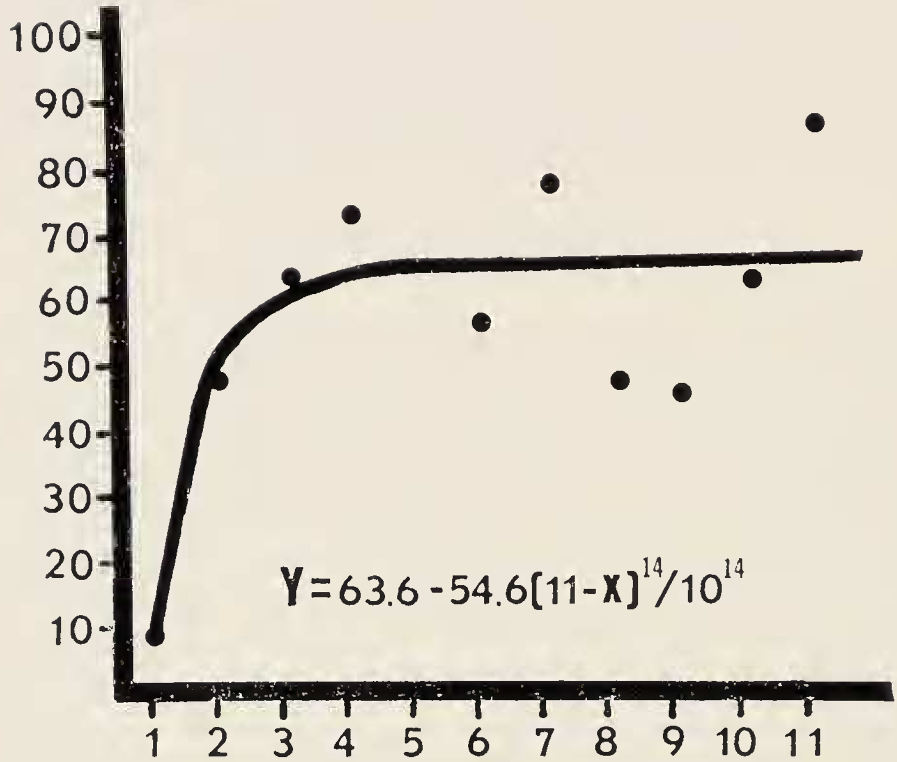

FIG. 1. Habitat use overlaps between Savannah and Grasshopper sparrows plotted over an 11-week period beginning the first week of May 1977. Values are expressed as a percent with 100% representing complete overlap and 0% representing lack of overlap.

All of the variables, except litter depth, did have a significant change with time, while there were no significant species × time interactions (Table 1). Except basal area cover, which has negative changes, and litter depth which did not change, all of the variables had positive changes with time, indicating growth of the vegetation.

When all of the variables were analyzed simultaneously (MANOVA), it was found that there was a significant ($P < 0.01$, $F = 7.28$) change in the habitat over time and that the species were significantly different ($P < 0.01$, $F = 2.48$) from each other in their breeding territories over time. As with all of the univariate interactions, the multivariate time × species interaction was not significant ($F = 1.10$).

The Vesper-Savannah sparrow and Vesper-Grasshopper sparrow pairs did not show any obvious temporal changes in their multivariately determined habitat use overlaps (Table 2). However, in the Grasshopper-Savannah sparrow pair a pattern did emerge (Table 2 and Fig. 1). Habitat use overlap started out to be small, showed a rapid increase and then leveled out. This indicates a distinct separation of habitats early in the breeding season when the birds first arrive. However, by the peak of the breeding season, overlap has increased greatly. A regression line (r =

TABLE 2

PAIRWISE MULTIVARIATELY DETERMINED HABITAT USE OVERLAP VALUES BASED ON 11 VEGETATION STRUCTURE VARIABLES MEASURED WEEKLY

Week	Savannah Sparrow Grasshopper Sparrow	Savannah Sparrow Vesper Sparrow	Grasshopper Sparrow Vesper Sparrow
1	9	—	—
2	48	37	62
3	62	68	35
4	72	37	52
5	63	66	28
6	56	36	18
7	76	20	60
8	47	51	42
9	45	31	33
10	63	42	50
11	86	58	42

0.917, $P < 0.01$) can be drawn through the points emphasizing the nature of the change.

Comparing the vegetation of the territories when the birds arrived with that of the peak of breeding activity, shows some interesting relationships. Overall, the territories of each of the species show significant ($P < 0.01$, $F = 6.49$) differences between the 2 periods. This change can be attributed to general differences in percent basal area cover of grass, forb height, vertical density of grass, effective height of vegetation and total grass density (Table 3).

DISCUSSION

Generally, early measurement of territories of the sparrows showed a gradient from open, or sparse grassland with low grass and forb densities, and high bare ground cover to high grass and forb density, and low bare ground cover. Vesper Sparrows occupied areas at the low end of the gradient; Savannah Sparrows were intermediate and Grasshopper Sparrows were at the high end, in the densest vegetation. These relationships were maintained into the breeding season in roughly the same order. The magnitude of difference, as measured by p-dimensional habitat use overlap, remained approximately the same for 2 pairs of species. However, while their positions on the gradient remained the same, Grasshopper and Savannah sparrows showed a marked change in the amount of structure held in common. That is, as the season progressed and the vegetation grew, their territories began to resemble each other, even though the birds hadn't moved. What started out looking like 2 separate habitat types ended up

TABLE 3

VALUES ($\bar{x}$ AND SD) FOR VEGETATION STRUCTURE VARIABLES FOR THE TERRITORIES OF EACH SPARROW SPECIES FOR 2 TIME PERIODS; NEAR ARRIVAL DATE AND DURING THE "PEAK OF BREEDING ACTIVITY"

	Arrival time					
	Vesper Sparrow		Savannah Sparrow		Grasshopper Sparrow	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Percent basal area cover of grass	17.10*	6.98	34.15*	41.37	29.37*	9.74
Percent forb cover	5.54	4.14	7.95	5.30	9.59	6.74
Percent litter cover	53.36	20.64	64.35	6.15	72.91*	18.25
Percent bare-ground cover	44.16	20.64	14.70*	6.65	25.62	17.92
Litter depth (in cm)	1.03	1.15	1.26	1.06	2.07	1.19
Forb height (in cm)	8.13*	5.41	7.93	3.16	6.47*	1.84
Effective height (in cm)	26.25*	5.17	25.00*	7.07	31.00*	7.38
Vertical density of grass	7.62	4.69	9.50	3.54	10.70	3.37
Vertical diversity of grass	0.54*	0.09	0.55*	0.09	0.64*	0.20
Horizontal diversity of grass	0.57	0.31	0.49*	0.11	0.73	0.21
Total grass density	48.50*	27.69	93.50*	3.54	108.60*	40.08

	Breeding peak					
	Vesper Sparrow		Savannah Sparrow		Grasshopper Sparrow	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Percent basal area cover of grass	6.25	9.91	9.35	11.94	5.29	4.61
Percent forb cover	13.77	12.11	12.90	10.34	16.93	13.09
Percent litter cover	56.20	30.61	71.02	19.72	85.97	12.84
Percent bare-ground cover	43.80	30.61	28.58	19.65	13.94	12.88
Litter depth (cm)	1.01	0.57	1.08	0.76	1.51	0.49
Forb height (cm)	13.62	6.39	10.03	4.24	12.88	5.75
Effective height (cm)	53.33	20.61	65.56	16.67	65.45	18.64
Vertical density of grass	9.67	6.52	11.44	4.93	13.45	4.97
Vertical diversity of grass	1.10	0.34	1.31	0.33	1.12	0.33
Horizontal diversity of grass	0.60	0.37	1.03	0.43	0.86	0.24
Total grass density	89.33	51.19	157.44	90.77	169.64	58.52

[1] * indicates that this variable shows a significant ($P < 0.05$) change from week 1 to week 6 for an individual species.

being nearly identical. In fact, Savannah and Grasshopper sparrow territories were significantly different from each other at week 1 (DFA, $P < 0.01$, F = 2.98) but not at week 6 (F = 0.86) or week 11 (F = 0.20).

Wiens (1974) has shown that early arriving Savannah and Grasshopper sparrows select territories that are vegetationally distinct, but that, after the breeding populations stabilized (mid-June), the territories were quite similar. It should be noted that all of his vegetation measurements were made in mid-June. My study does not take into account the time of territory occupancy but does show that vegetation growth can account for statistically significant changes in species specific habitat requirements.

Harner and Whitmore (1977) have shown that the number of variables entered into the model can affect the community patterns obtained. It now appears that the time of measurement can also be a factor affecting these patterns. An investigator measuring bird habitats only during a limited portion of the breeding season could produce results that are strikingly different from those of an investigator collecting data in a period differing by only a few weeks. Moreover, if the vegetation data are collected over an entire breeding season, then some method of factoring out the time effect must be used (Green 1974).

This study also shows that the habitats selected in early spring are for the most part structurally different from those into which the young are fledged after breeding. There is strong evidence that in many bird species, primary emphasis is placed on learning or imprinting during the early nesting state (Klopfer 1963, 1965; Klopfer and Hailman 1965; Hildén 1965; Orians 1971). This could lead one to ask what cues are learned by the fledglings that allow them to select adequate habitats the following spring?

Perhaps those characteristics of the habitat which change radically with time provide little information in the selection of habitats, while those that remain constant, or nearly so, can be learned and remembered when the fledglings come back the following spring. Perhaps a fruitful line of research might be to manipulate certain variables, litter depth for example, that do not show a marked change with time in order to determine their role in habitat selection.

SUMMARY

In order to determine the effect of vegetation growth on bird community patterns, territories of Grasshopper, Vesper and Savannah sparrows breeding on reclaimed surface mines in West Virginia were studied during the summer of 1977. Eleven vegetation structure variables were measured weekly on each territory for 11 weeks during the breeding season. All variables, except litter depth, changed significantly during the study period. Multivariately determined habitat use overlap values showed that Grasshopper and Savannah sparrow habitats, after starting out to be quite distinct, became more similar in structure as the season progressed, going from 9% overlap in May to 86% overlap in July. It was found that habitats for all 3 species measured near the arrival date were statistically different from those measured in mid-June, at the "peak of breeding activity." Therefore, the habitats actually selected differed from those into which the young are fledged.

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